ON PHYTONISM [1])

by

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In botanical literature one may more than once meet with the idea that the stem of vascular plants consists of the basal parts of leaves, or as the view is called with phytonism.

If one wants to know anything about the evidence on which this phytonism is based, one will soon find out that this is not so easy, and that the literature on phytonism is of a very disappointing kind.

One of the first peculiarities striking the attentive reader is its incoherency. None of the authors build on the evidence brought forward by their predecessors: each one starts anew and at best cites the names of some previous writers, without mentioning the titles of their works, let alone their arguments.

The explanation of this curious fact must be sought in my opinion in the circumstance that phytonic ideas are not so much the outcome of investigation as the consequence of a philosophical tendency to simplify our conceptions. The real content of several phytonic papers simply consists in the expression of the phytonic view; this may be accompanied by the introduction of new names.

[1]) Somewhat extended form of paper read before section M of the Fifth Botanical Congress at Cambridge 1930, as an introduction to the discussion on phytonic theories.

Under these circumstances I shall not try to give a thorough survey of the literature, which goes back at least to 1800 [1]), but I shall only discuss the works of those three phytonists who are often cited as the founders of phytonism, viz Gaudichaud, Schultz and Delpino.

Ch. Gaudichaud [2]) wrote a 4° book of 130 pages (81 of which contain only the explanation of the 18 plates). In this work we find a good deal of not over-accurate observation on the course of vascular bundles in seedlings, on the course of fibres in woody plants, on anomalous secondary thickening, etc. The relation between these observations and phytonism does not become clear to the reader; Gaudichaud seems to see the proof for phytonism in the fact that leaf traces are continued into stem and root. On the same lines we might infer that a house belongs to the water company if the service-pipes extend into it. Every phyton according to him consists if fully developed of four parts: the „mérithalle limbaire", the „mérithalle petiolaire", the „mérithalle tigellaire" and the „système inférieur", or root part.

The second of our leading phytonists was C. H. Schultz. I must confess not to have seen his work [3]), which was not at my disposal. We have however a very extensive criticism on it by no less an authority than Hugo von Mohl [4]). We learn from this that Schultz makes no real difference between stem, leaf and root, but that all three are formed by one kind of parts, the anaphytes,

[1]) E. Darwin, Phytologia, or the philosophy of agriculture and gardening, London, 1800 (cited after A. Braun Das Individuum, Berlin 1853).

[2]) Recherches générales sur l'organographie, la physiologie et l'organogénie des végétaux. Paris 1841.

[3]) Die Anaphytose oder Verjüngung der Pflanzen. Ein Schlüssel zur Erklärung des Wachsens, Blühens und Fruchttragens, mit praktischen Rücksichten auf die Cultur der Pflanzen, Berlin 1843.

[4]) Botan. Zeitg. Vol 1, 1843, col. 667.

which are capable of living independently. Stem, leaf, and root therefore can change into one another. Every internodium constitutes one anaphyte, every leaf is another one, a compound leaf is even formed out of several anaphytes.

There is thus as we see a striking difference between this anaphytosis and Gaudichauds phytonism; the stem does not consist of fused leafbases but of its own elements, apart from those of the leaves. Evidence for these views seems not to have been given by Schultz.

Mohl concludes his elatorate and well argued review with the remark that the principle idea of Schultz is erroneous, and tends to bring science into a state of confusion.

Our third phytonist was F. Delpino, who in 1880 published a preliminary note [1]) and in 1883 a whole book on phyllotaxis [2]).

In both papers it is proved „con tutto rigore di logica" that the stem does not exist, but that what had been considered up till then as stem is only a union of leaf bases. The „proof" of this (and of many other theorems, e.g. that there must be an triangular apical cell in shoots of Phanerogams) consists in the famous „pila sferotassica", a pile of spheres.

Delpino experimentally found it possible to stack up spheres in a spiral in such a way that no continuous open space in the axis of the pile was left, the arrangement of the spheres being more or less similar to that of the leaves in a phyllotaxis of the main series. By this „esperimento decisivo" phytonism was established!

[1]) Causa meccanica della fillotassi quincunciale. Nota preliminare. Genova 1880.

[2]) Teoria generale della fillotassi. Atti della R. Università di Genova Vol 4 P. 2 Genova 1883.

Lateron Van Iterson [1]) proved mathematically that in the pila sferotassica of Delpino a small open space in the axis is always present. We do not need this however to understand that Delpino's „proof" was only a very remote and unsubstantial analogy, and that the whole base of Delpino's phytonic theory was, to put it mildly, extremely weak. There exists in phytonic literature however one single paper of quite another description, a work of a scientific character, by L. J. Čelakovský. This paper [2]) contains excellent argumentation, based on a vast knowledge of facts: we shall therefore have to consider it with due interest.

It is however worth while to point to the curious fact that this paper has pretty well been ignored or even spoken lightly of by later phytonists. Evidently it was not to their taste; they were more satisfied by the writings of Schultz and Delpino.

We see this clearly in the historical paragraph on phytonism in the handbook [3]) of J. Velenovský, which I cannot refrain from citing here. „Schon J. W. Goethe [4]) (1790), später E. Meyer (1832), Wigand (1846) geben zu, dass die letzte Einheit, aus der die Pflanze sich zusammensetzt, das Blatt sei. Deutlich hat diese Theorie C. H. Schultz (1843—1847) ausgeführt, welcher sagt, dass der Stengel der Pflanze sich aus den zusammengewachsenen Blattbasen zusammensetzt [5]), denen sich seitwärts das eigentliche Blatt anfügt. Den zusammengewachsenen Stengelteil samt dem zugehörigen Blatte nennt

[1]) G. VAN ITERSON JUN. Mathematische und mikroskopisch-anatomische Studien über Blattstellungen nebst Betrachtungen über den Schalenbau der Miliolinen. Jena 1907.

[2]) Die Gliederung der Kaulome Bot. Zg. 59, 1901 p. 79.

[3]) Vergleichende Morphologie der Pflanzen, Prag 1905—1913, on p. 551.

[4]) Who never enounced phytonic ideas.

[5]) cf. above p. 84.

er Anaphyt [1]). Der französische Forscher Gaudichaud (1841) sprach fast gleichzeitig dieselbe Theorie aus, nur dass er seine Stengelteile mit der Bezeichnung Phyton belegt. Am vollkommensten [1]) hat diese Lehre in der jüngsten Zeit auf Grund der Phyllotaxie [1]) Delpino (1883) erläutert. Er nennt seine Glieder Phyllopodien. Für die Theorie Delpinos hat sich auch De Vries ausgesprochen. Čelakovský war stets ein eifriger Verteidiger der Anaphytosentheorie und veröffentlichte in dieser Beziehung drei Arbeiten, in denen er jedoch zu den bestehenden Theorien nichts neues hinzugefügt hat".

So much for the more or less phantastic phytonic literature. I trust this will suffice for most botanists. We see that phytonism has many shapes, and there are certainly still others to be found in the literature. The common point however seems to be that the existence of the stem as an independent member of the plant body is denied. It is to this idea of phytonism that I wish to confine my arguments.

I have now first to mention the arguments brought forward by Čelakovský, and to discuss their value. As no serious review of them has been published in botanical literature as far as I know, this may be of some use. Čelakovský himself brings his arguments into six groups [2]), which I will discuss one after the other.

1. The first is taken from the development of the monocotyledonous embryo. Here the cotyledon and the main root are from the first opposite, the first leaf arises at the side of the solid stretched embryo. The second leaf in its turn may arise in the same way pleuroblastically as a lateral outgrowth of the first leaf; this pleuroblastic formation may continue up to the 7th or 8th leaf. Sooner or later however, often directly after the formation of the

[1]) cf. above p. 84.
[2]) l.c. p. 101.

cotyledon, the vegetative cone appears, and the pleuroblastic formation is replaced by the acroblastic manner.

Here we have, according to Čelakovský, phytons, increasing in number by budding, like yeast cells. He has of course to explain the nature of this vegetative cone, which occurs so generally in vascular plants. Here he points to his phytostatical law, by which term he designates the fact that in embryonic tissue a strong lateral body will always push aside a weaker original apex.

If the young phytons produce daughter phytons in early stages of their development and especially when the young phytons only develop their basal part and still lack a leafy outgrowth, the meristematic tissue of these young phytons may look like a single body, which may have a greater bulk than the leafy outgrowth of a phyton when this makes its appearance. This is nearly always the case, only in the monocotyledonous embryo where the leaves are laid down one by one and apparently slowly at first, the multiplying phytons are clearly to be seen.

We may grant that in this way the facts might be explained. The phytostatical law is surely of general validity; it may itself be explained from the stretching forces in growing embryonic tissue. We might however remark that if the common view is right that the leaves arise on the surface of the stem, the monocotyledonous embryo with its big cotyledon and small plumula should show us the actual shape, because by the phytostatical law the cotyledon would push aside the weak plumula. The facts are just as much in accordance with phytonism as with the classic views: the question is not to be settled in this way.

2. Čelakovský takes it as an established fact that the monocotyledonous embryo is to be derived from the sporogon of *Hepaticae*, by a process of sterilisation. This belief was prompted by a too high estimation of the antithetic alter-

nation of generations; it was taken that a sporophyte could never be the homologon of a gametophyte and even that neither of them could ever acquire properties of the other.

3. In some cases we seem to have free phytons (Čelakovský calls them Sprossglieder, shoot-members). As instances he cites the male flowers of *Lemna* and *Zanichellia*, the female flowers of *Balanophora* and *Araucaria*, and as vegetative part the body of *Lemna*. He remarks himself however [1]) that all these cases have been explained in different ways, so that many botanists will still have their doubts about them.

We certainly must agree that these cases of excessive reduction cannot be regarded as evidence of the phylogenetic origin of shoot and leaf. And as phytonism is essentially a phylogenetic conception, we may disregard these cases.

4. The sympodia of *Ampelidaceae* and the cincinni of *Boraginaceae* give strikingly analogous cases to a stem built from leafbases. In all we have an apparently simple vegetative cone; yet in the sympodia just mentioned we have good evidence that they consist of series of shoots, each one being a branch of the preceding one. These instances make it especially clear that an ordinary stem apex in its turn might just as well consist of a number of phytons, one producing the other but nevertheless looking in the young state like a single body.

A proof of the reality of phytonism is however not to be obtained in this way: it only proves the possibility of it.

5. The leafy stem of mosses arises from the protonema by a change in the segmentation of the apical cell. The protonema, consisting of one single row of members, then changes into the leafy stem and the holocyclic growth is replaced by the mericyclic growth.

[1]) l.c. p. 88.

Against this argument we might simply remark that the leafy stem of mosses need not be a homologon of the shoot of vascular plants, not because of its belonging to a gametophyte, but because of the remote positions of mosses and vascular plants in the vegetable kingdom.

But even if we do not want to discard this case for such a reason, we can never get evidence for phytonism out of it. We have only an analogy to the case, not uncommon in vascular plants, that a stem with well developed amplexicaulous leaves and „holocyclic" internodes changes higher up into an inflorescence with many bracts with narrow insertions, so that a „mericyclic" condition ensues. The classic view is quite able to explain this and there is no need of a phytonic conception.

6. The shootmembers, the existence of which in Phanerogams is only concluded as a result of abstract reasoning, are clearly to be distinguished in Mosses and Pteridophytes in the shape of the segments of the apical cell, in as far as they form the leaves.

As Čelakovský himself adduces, in many Pteridophytes the relation between segments of the apical cell and leaves is lost: this might however be a tendency to an early division of the segments into cells and an approach to the mode of apical growth which prevails in Phanerogams.

On this argument I might say: if the stem were formed out of phytons, the segments really might be the phytons. We should then expect however that wherever the segments were to be discerned they would correspond in number and position to the leaves. The well known case of *Equisetum* shows that this does not hold good.

If on the contrary the classic view is right, the case of *Equisetum* would not offer a problem at all. And the case of *Ceratopteris* which Čelakovský cites, where every segment of the triangular apical cell develops a leaf, may be explained just as well, in the same way as in the leafy

moss stem, viz. by assuming that the leaves are laid down in a certain phyllotaxis inside the apical cell, and that the first visible result of the activity of the new leaf is the cell division which leads to the formation of a new segmental wall.

Summing up the evidence brought forward by Čelakovský, we may say that he has shown that phytonism might be in accordance with the facts, or expressed in another way that it is possible to construct a scheme of thought which fits in with phytonism and with many facts. This is much more than any phytonist did before.

He has however not brought any decisive proof that phytonism is to be taken as a truth, since all the facts may be very well explained otherwise.

To settle the question whether phytonism is to be accepted or rejected, we must therefore look for further conclusive evidence, either from palaeobotany or from the study of recent plants.

Palaeobotany might give a direct decision if only we knew more about fossil plants. As far as our knowledge goes at present, the fossils do not give the slightest evidence in favour of phytonism. If the modern view is confirmed that the origin of leaves is to be witnessed in *Psilophytinae*, the stem is pre-existent to the leaf, so that no room is left for any phytonic theory. However probable this may be, we shall have to wait for more evidence before we can consider phytonism as completely refuted; we can only say that strong evidence in favour of phytonism should be brought forward in order to neutralize the serious objections raised against it by palaeobotany.

Now I hope to be able to show — and that is the aim of this paper — that even the organisation of the recent plants can supply the proof that the phytonic theory is wrong, in so far as it is inconsistent with the facts of phyllotaxis. Phyllotaxis demands that the phytons are

arranged in a definite way. Now we may either suppose that the phytons, after having been formed in the multicellular vegetative cone of Phanerogams, are freely movable in the apex and may settle down in any convenient place, or we may suppose that they occupy more or less the same region from the beginning. As the cells in the apex do not shift this last supposition seems more natural.

If we consider this view first, we must try to realize how the different leaf arrangements may be brought about.

We can for this purpose divide the possible arrangements into three groups: the regular spiral phyllotaxis, the regular whorled and the irregular phyllotaxis. As all these three exist, the origin of each must be conceivable.

The regular spiral phyllotaxis, with its genetic spiral, might be brought about in this way, that every phyton number n produced one single daughter phyton number $n + 1$ at such a distance as the divergence requires; the genetic spiral would constitute a real chain of coherent phytons. This supposition cannot give the general solution; when we think of a large sunflower head with a Fibonacci spiral, bract n is separated from $n + 1$ by a great number of other bracts. There is no possibility of contact between two successive numbers unless we have recourse to the view of Delpino and Velenovský that every phyton forms a complete transverse slice of the stem, so that all phytons are only in contact with the next lower and higher number. In a sunflower head with a $34 + 55$ phyllotaxis there would be in this way 88 internodia between a given bract and the next one above it, every internode being about 50 μ thick, less than the dimensions of one single parenchyma cell.

And an *Anthurium* spadix with a $8 + 13$ system, changing at a given point into a $8 + 12$ one would suddenly have no genetic spiral any more, but instead of it four spirals with a much smaller divergence; whereas the internodia

would suddenly be four times as thick and would no longer bear only one, but four flowers at a time.

If we do not want to take all this for granted, we have to suppose that the regular spiral phyllotaxis may be built up in some cases only according to the genetic spiral, viz., in those cases where the successive members are in mutual contact. In the more complicated cases we may however suppose that the phytons produce daughter phytons in the direction of one set of contact parastichies. This would meet many of our objections. Yet there would remain the following ones. As there are always at least two sets of contact parastichies we should be obliged to suppose that these had different characters.

Now we see that parastichies may be lost or added in both directions in one and the same object, which is distinctly unfavourable to this view.

Another difficulty would remain in the rising and falling phyllotaxis. A $2+3$ system may change into a $3+5$, $5+8$, $8+13$ system etc. If the contact parastichies were the real causes of the phyllotaxis we should have to suppose that 3 of these rows of phytons, 3 chains, might be replaced by 8 in such a way that two of the three were each replaced by three steeper ones, and the third by two.

Analogous difficulties would rise for the regular whorled systems. In a $6+6$ system we should have to suppose either six left-hand winding phyton chains or six right-hand ones; the observation does not however reveal any difference between the two sets of contact parastichies.

The irregular systems present new difficulties to phytonism. It is a well known fact to students of phyllotaxis that in many irregular systems (spadix of *Anthurium* e.g.) there are contact parastichies to be seen which however do not run in a constant direction, but in many cases in a curve. This curve may sometimes have such a course that in following it upwards we not only reach a horizontal

part, but even at a downward-running slope. It is clear that in such cases the parastichies can never be rows of daughter parastichies. Yet the regular and the irregular cases have so much in common and the transition between the two are so numerous and so gradual, that the governing law must be the same in both.

We may resume the foregoing in this way. The multiplying phytons must be arranged in a regular way. The regularity cannot be the consequence of the formation of a continuous chain of phytons according to the genetic spiral, nor can it be the outcome of the formation of many such chains according to the contact parastichies. The only way to explain the existing regularity in immovable phytons is to suppose that they are formed in the largest open spaces over the existing ones, as Hofmeister did for the leaves.

This however is quite feasable for leaves arising as secondary formations on a stem apex, not for phytons, which must be present at a given moment in a definite number, packed together without interstices so as the form the whole vegetative cone.

We may now look for a relief in the supposition of movable phytons, being at first irregularly arranged and assuming their due positions later on. This idea would fit in with the rule of Hofmeister. But how are we to picture to ourselves the densely packed and yet freely moving phytons in a meristem with fixed cell boundaries?

If there were a certain medium, a glue between the phytons, the idea would perhaps lose some forbidding aspects. But at the same time phytonism in the strict sense would have been abandoned, as the glue would be the preexistent stem again.

Now we saw before that palaeobotany had no evidence in favour of phytonism, but that the evidence against it was pretty strong, and that from the morphology of recent

plants no arguments in favour of phytonism were to be derived. When we now find that the facts of phyllotaxis are not to be reconciled with phytonism, we may safely drop the phytonic theory altogether.

We may do this the more readily, as there is no need of any such theory: the ordinary classic view of morphology of vascular plants is quite sufficient and there are no serious difficulties in the organisation of the shoot for which a phytonic theory is required.

At the apex of the stem new leaves arise in places which are determined according to the rule of Hofmeister. These leaves may extend over the surface so as to come into mutual contact, but this is not necessary. They may even terminate their development at any stage.

Terminal leaves such as the cotyledon of the grass embryo in the young state, of the stamen of *Euphorbia* in the adult state, do not give rise to any difficulty, as they are explained by the phytostatic rule of Čelakovský.

Cases like the cincinnus where a branch system has apparently a simple vegetative point, built up from several branches, are easily to be understood. Every member originates in the axil of a prophyll of the next lower member. But as the new members do not yet develop visible protuberances, they simply form meristematic areas, and the boundaries between the parts only become visible when the members grow out. In contrast to the hypothetical phytons constituting the stem apex, the members of a cincinnus from the beginning show perfectly clear genetic relations, which have never been misunderstood.

In literature the perikaulom [1]) and leaf-skin [2]) theories

[1]) H. Potonié Grundlinien der Pflanzenmorphologie im Lichte der Palaeontologie. Jena 1912.

[2]) e.g. E. R. Saunders. The leaf-skin theory of the stem: a consideration of certain anatomico-physiological relations in the Spermophyte shoot. Annals of Botany 36, 1922, p. 135.

are often linked up with phytonism. In these conceptions stem and leaves are taken as different organs, hence our objections to phytonism do not apply to them.

The only difference from the ordinary view is that the boundary between leaf and stem is not sought at the place of the later leaf scar, but is placed more towards the interior, so that the whole cortex or even more is considered as parts of the leaves.

These theories certainly contain a deal of truth. During the development of the shoot the original leaf cushion is much extended, and the later leaf scar will usually be quite another boundary than the demarcation between the leaf primordium and the underlying stem in the young condition.

Yet we must not go too far, and we are not justified in calling the whole cortex a product of leaf bases. In the numerous cases where free areas are left between the leaf primordia [1]) these areas develop a normal cortex with a normal epidermis, although they never belonged to any leaf.

And further, if leaf and stem are different organs, but the one develops on the surface of the other, it is clear that there will never be a definite demarcation between them. Neither in the first stages nor in the full grown leaf can we exactly say where the leaf ends and the stem begins.

I therefore cannot see any advantage in the adoption of these views.

Of course it will be highly interesting if we can get any insight into the phylogenetic origin of stem and leaf. Perhaps palaeobotany will furnish us with definite proof of what now seems only very probable, that the leaves of

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[1]) cf. the chapter „Zeichnung und Form des reifen Stengels' on p. 230 of VAN ITERSON l.c.

macrophyllous plants have sprung from lateral branch systems like the fertile stems of *Asteroxylon*.

Perhaps still another solution will be given, but I am convinced that the development of our knowledge will not lead to any phytonic idea or to any leaf-skin theory.

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